

BOOK REVIEWS

Action Potentials Reconsidered

Spikes. Exploring the Neural Code. FRED RIEKE, DAVID WARLAND, ROB DE RUYTER VAN STEVENINCK, and WILLIAM BIALEK. MIT Press, Cambridge, MA, 1996. xviii, 395 pp., illus. \$45 or £38.50. ISBN 0-262-18174-6. Computational Neuroscience. A Bradford Book.

About 70 years ago, the physiologist E. D. Adrian reported his observations on the response of single muscle stretch receptors to a fixed load. He found that the number of action potentials (spikes) recorded during 10 seconds increased as the load on the receptor increased. Subsequent observations confirmed that in a very wide variety of sensory systems the spike rate increased with stimulus intensity. These now-classic observations laid the foundations for what has become the standard model of the neural code in modern neuroscience. Rate coding, as it is sometimes called, is the notion that the average rate encodes the "message" in a neuronal spike train and that this message can be "decoded" by simply counting the number of spikes in some long time window.

Spikes: Exploring the Neural Code challenges the standard model. The epilogue, "Homage to the single spike," neatly summarizes the book's theme: "Individual spikes are important." It continues, "The individual spike, so often averaged in with its neighbors, deserves more respect." As we arrive at this epilogue after almost 300 pages of thoughtful arguments, we are compelled to agree.

One of the main arguments is that neuroscientists have emphasized neuronal responses to stimuli devoid of interesting temporal structure. Adrian, for example, studied the responses to prolonged (seconds long) muscle stretch; yet the stretch imposed by a frog's jump is orders of magnitude briefer. Behaviorally relevant decisions must often be made very quickly, leaving time for just one or two spikes. Thus though it makes sense to speak of an "average" spike rate during a one-second response, we need to think carefully about what "average" rate means when the average is over so few spikes.

The authors muster a wealth of experimental data to support their challenge and develop the theoretical and mathe-

matical tools required to appreciate it. The book is a joy to read, as both the theoretical and the experimental results are presented with respect, precision, and clarity. The first chapter briefly summarizes the history of neural coding, through the seminal work of Adrian through the present. The second chapter lays out the mathematical foundations for characterizing neuronal responses. Chapters 3 and 4 form the core of the book. Chapter 3 shows how information-theoretic techniques can be used to quantify rigorously how much information a spike train from a sensory neuron conveys about the stimulus. Chapter 4 argues that the nervous system operates near the physical limits imposed by noise in the sensory input. The fifth and final chapter proposes future directions in which work on the neural code will (or should) proceed and is followed by a nearly-100-page mathematical appendix.

The authors of the book are all physicists by training, so it is no surprise that the text is very mathematical, written in the dialect of mathematics favored by physicists (rather than, for example, by signal processing engineers). All the arguments are carefully developed, and the book should be completely accessible (albeit with a bit of work) to anyone who has had an undergraduate-level training in physics, engineering, or mathematics. The approach and the conclusions are of such importance, however, that it will be read by a much wider audience of motivated neuroscientists—anyone interested in issues of neural coding—even some readers will be unable to follow some of the arguments in detail.

The only criticism to be made of this book is that we are left wanting more. The book provides such a compelling framework for understanding sensory processing in single neurons that one would like to see how far it can be extended. We would ask for more about the techniques required to analyze data from simultaneous recordings of dozens or hundreds of neurons (there is only a brief section devoted to this); about the computations that occur beyond the earliest stages of sensory processing; and about the output (motor) end of the brain. Let us hope for an encore.

This book will undoubtedly become a classic. The ideas presented in it have al-

ready begun (in no small part through the work of the authors) to reshape our views of the neural code. This book will make them accessible to a much wider audience.

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Development and Diversity

Cells, Embryos, and Evolution. Toward a Cellular and Developmental Understanding of Phenotypic Variation and Evolutionary Adaptability. JOHN GERHART and MARC KIRSCHNER. Blackwell Science, Cambridge, MA, 1997. xiv, 642 pp., illus., + plates. Paper, \$69.95 or £29.50. ISBN 0-86542-574-4.

New paradigms in science set the stage for major advances in research and understanding. Such a change occurred when homeoboxes were discovered in the middle of the 1980s and similar sequences, and genes, were rapidly identified in many animal species. Developmental biologists gradually came to realize that molecular mechanisms for fundamental biological events must have predated the major burst of multicellular diversity in the Cambrian era. Although the implications of this paradigm shift have been building for the last 15 years and a few books have already appeared that make it the central theme, Gerhart and Kirschner's *Cells, Embryos, and Evolution* is remarkable for breaking new ground. More than 10 years ago, as the authors were attempting to write a modern book on developmental biology, new discoveries were continually pointing to the amazing conservation



"A marine flatworm, *Pseudoceros ferrugineus*, Coral Bay, Australia. Phylum Platyhelminthes. Triploblastic, bilateral symmetry, a blind gut, light sensitive eye spots, a ladder-like nervous system, and no coelomic cavity. Development involves spiral cleavage and a 4d blastomere as the source of mesoderm. Length, 2–8 cm." [From *Cells, Embryos, and Evolution*; A. Flowers and L. Newman]

of developmental mechanisms. Instead of writing the originally intended book, the authors recognized the possibility of presenting a more unified view of the subject. As their subtitle indicates, this would be directed "toward a cellular and developmental understanding of phenotypic variation and evolutionary adaptability." The authors propose "to understand the molecular and genetic changes most important for the metazoan radiation, to identify how the cell and developmental biology of these organisms accommodated to change and were changed by them, and to appreciate how conserved cellular and developmental mechanisms might have played a role in major modifications of anatomy and physiology"—in other words, to understand how phenotype and genotype are connected. They have been amazingly successful in this effort.

The book falls into two major sections. The first half expounds a number of key cellular properties or processes that underlie the evolution of organisms. The authors begin their discussion with a consideration of the similarities and differences between prokaryotes and eukaryotes. Prokaryotes have diversified with extremely varied metabolic functions, but eukaryotes, while retaining basic cellular mechanisms, have through the formation of epithelia and matrix molecules made the critical transition to complexity of cell types and functions. The authors, in an interesting fashion, propose far-reaching consequences for a few key properties possessed by multicellular animal forms. Both intercellular signaling systems involving calmodulin-mediated calcium responses, G-proteins, or protein kinase cascades and the upstream regulatory region of genes (which "resembles a battlefield, with positive and negative inputs contending for the RNA polymerase at the promoter") are shown to be characteristic of a wide variety of multicellular processes and developmental events. The authors adopt the term "contingency" to characterize the dependence of these processes on prevailing conditions. In a separate chapter they expand on the concept of "exploratory behavior" in a variety of biological processes to account for evolutionary diversity and success. At the molecular level, microtubule function during mitosis illustrates this principle. Unstable microtubules probe the cell until stabilized by attachment to kinetochores. This well-established dynamic instability provides a

mechanism for establishment of the ordered spindle from the random organization of chromosomes in the premitotic cell. At the cellular level, a similar extravagance of randomness in nerves, lymphocytes, blood vessels, and trachea provides the mechanism for a regularity of pattern and function. The key insight here is that developmental exploratory principles provide the mechanism for adaptation to new situations as well as for insulating the organism from deleterious consequences of minor mutations.



"The acorn worm, *Ptychoderna flava*, from Lizard Island, Australia. Phylum Hemichordata. This filter feeding deuterostome possesses gill slits, a short dorsal hollow nerve cord sometimes equated with the nerve cord of chordates, and a stiff stomochord in the [pharynx] sometimes equated with the notochord. Length, 6 cm." [From *Cells, Embryos, and Evolution*; A. Flowers and L. Newman]

The second half of the book begins with an exposition of phylotypic body plans and elaborates on how the insights of modern cell and developmental biology provide a potential understanding of the mechanisms underlying these body plans. Here the authors draw on a few well-understood phenomena, such as the evolution of the chordate limb or the flexibility inherent in developmental processes such as the neural crest, to provide broader models of how the diversity of multicellular animal species can have been produced through developmental change.

Though the book is long and sometimes wordy and there are occasional textual errors or faults in the artwork, I find it a stimulating effort to give a unitary perspective on evolutionary mechanisms responsible for today's complex biosphere. I hope there will be future editions as well as extensions by others. Clearly, we have reached a state of experimental biology where this exercise is fruitful.

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Browsings

Discovery of the Magnetosphere. C. Stewart Gillmor and John R. Speiter, Eds. American Geophysical Union, Washington, DC, 1997. vi, 286 pp., illus. \$55; to AGU members, \$38.50. ISBN 0-87590-288x. History of Geophysics, vol. 7.

Work of the late 1950s and 1960s as recalled by some 25 "pioneers."

The Eye and Visual Optical Instruments. George Smith and David A. Atchison. Cambridge University Press, New York, 1997. xii, 816 pp., illus. \$94.95 or £90, ISBN 0-521-47252-0; paper, \$54.95 or £35, ISBN 0-521-47820-0.

A textbook that emphasizes those instruments—including ophthalmic lenses, microscopes, telescopes, projection systems, and vision-testing instruments—in which the eye is an essential component in the imaging process, with consideration also of the camera and visual ergonomics.

Organizing Scientific Meetings. August Epple. Cambridge University Press, New York, 1997. xiv, 184 pp. \$44.94 or £32.50, ISBN 0-521-56351-8; paper, \$14.95 or £11.95, ISBN 0-521-58919-3.

Practical advice and cautionary tales on every aspect of the job, from whether to take it on in the first place to getting the proceedings published.

Stuff. The Materials the World Is Made Of. Ivan Amato. BasicBooks, New York, 1997. x, 294 pp., illus. \$25 or C\$35.50. ISBN 0-465-08328-5.

A journalist's breezy narrative of the transformation of "stuff" by humans, beginning with stone tools and proceeding to developments—polymers, ceramics, synthetic diamonds, fullerenes, semiconductors—that define the present-day field of materials science.

Summer for the Gods. The Scopes Trial and America's Continuing Debate over Science and Religion. Edward J. Larson. BasicBooks, New York, 1997. x, 318 pp., illus. \$25 or C\$35.50. ISBN 0-465-07509.

The story of the 1925 legal challenge to evolutionism and contemporary and subsequent commentary on the event by various parties, including country and western singers, literary figures, and academic historians.

Water, Rivers and Creeks. Luna B. Leopold. University Science Books, Sausalito, CA, 1997. xiv, 185 pp., illus. \$30. ISBN 0-935702-98-9.

In a revised version of his 1974 *Water—A Primer* a hydrologist of long experience explains the processes underlying the availability of this key resource.

Women's Health Research. A Medical and Policy Primer. Florence P. Haseltine and Beverly Greenberg Jacobson, Eds. Health Press International (American Psychiatric Press), Washington, DC, 1997. xxii, 364 pp. \$42.50. ISBN 0-88048-791-7.

An "educational resource" covering diseases as they affect women specifically and recent and desired policy changes, produced by the Society for the Advancement of Women's Health Research.